

AN ICHTHYOSAUR WITH PRESERVED SOFT TISSUE FROM THE SINEMURIAN OF SOUTHERN ENGLAND

by DAVID M. MARTILL

ABSTRACT. A new specimen of ichthyosaur in a carbonate concretion from the Sinemurian (Lower Jurassic) of Black Ven, near Charmouth, Dorset, shows soft tissue preservation. The specimen is indeterminate at generic and specific level. It comprises the posterior portion of the axial skeleton and displays a lunate caudal fin preserved as an organic film. A thin band of phosphatized muscle tissue in the dorsal lobe of the tail indicates that some control of fin attitude was possible despite the absence of axial skeleton in the dorsal lobe. This is the earliest record of an ichthyosaur with an indisputable complete lunate caudal fin. There was a progressive increase in the angle of downturn of the vertebral column in the ichthyosaur tail, from approximately 25° in the new specimen, to approximately 80° in Late Jurassic ichthyosaurs. Ichthyosaurs did not possess typical reptilian epidermal scales.

JURASSIC ichthyosaurs with soft tissues preserved have been described from several localities but are nevertheless extremely rare (Keller 1992; Martill 1993). Such specimens offer a unique opportunity to examine aspects of ichthyosaur morphology, biomechanics, physiology and ecology (Keller 1976; McGowan 1979; Riess 1986; Taylor 1987). The most spectacular specimens are from the *Posidonia* Shale of Baden-Württemberg, Germany from which many complete individuals with body outlines, stomach contents and juveniles within the body have been reported (Fraas 1892; Baur 1895; Hauff 1921; Broili 1942; Hauff and Hauff 1981; Böttcher 1989; Martill 1993). Less well documented examples occur in the Solnhofen Limestone (Upper Jurassic) of Germany (Bauer 1898; Martill 1993).

Despite the abundance of ichthyosaurs in the Lower Jurassic of England, very few specimens have been reported with soft tissues preserved. The best specimens appear to be from the Hettangian of Barrow-upon-Soar, Leicestershire (Lydekker 1889; Andrews 1924; Martin *et al.* 1986; Martill 1987*a*), but these are all incomplete, and are either limb outlines or small patches of organic material associated with the postcranial skeleton. No ichthyosaur with a complete body outline has been recorded from the British Isles. A new specimen from the Lower Jurassic near Lyme Regis exhibits the first ichthyosaur caudal fin to be reported from the British Isles. It is a remarkably preserved arcuate fin with prominent dorsal and ventral lobes and is described in the following account.

SOFT TISSUE PRESERVATION IN ICHTHYOSAURS FROM ENGLAND

The earliest account of ichthyosaurs with soft tissues preserved is that of Buckland (1836), who described patches of black material associated with skeletons from the Lower Lias of Lyme Regis, Dorset, and from Barrow-upon-Soar, Leicestershire. Buckland noted that the Lyme Regis specimens showed no evidence of scales, and suggested a comparison with the skin of modern frogs. Owen (1840, 1841) reported an ichthyosaur hind paddle with soft tissues from the Lower Lias of Barrow-upon-Soar, and showed that the soft tissues extended well beyond the limb skeleton. However, this is not borne out by Holzmaden specimens, which show the non-skeletal tissue to be restricted to the immediate region of the limb skeleton. Shortly afterwards, Pearce (1846) reported an ichthyosaur from Somerset with an embryo within the area of the trunk, and noted that soft

tissues were associated with the embryo. Mantell (1851) figured the hind limb described by Owen (1840) and commented that a second specimen with soft tissues preserved had been damaged during preparation. Mantell may have damaged the specimen himself, as later implied by Davies (1864) in a report of a further ichthyosaur from Barrow-upon-Soar with associated preserved soft tissues. Coles (1853) noted small black hook-shaped objects associated with an ichthyosaur from the Lias between Upton on Severn and Tewkesbury. He interpreted these as scales within the skin of the ichthyosaur, but it is clear from the figure of the specimen that these objects were cephalopod hooklets in the gut of the animal (see Pollard 1968). Later, Moore (1857, 1862) reported a nodule containing an ichthyosaur with gut contents and preserved soft tissues but provided no locality or horizon data. Subsequently further ichthyosaurs with soft tissues have been reported from Barrow-upon-Soar (Lydekker 1889; Andrews 1924), Lyme Regis (Whitewar 1956), an unknown locality in the Severn Valley (Delair 1966) and the Oxford Clay of central England (Martill 1987a, 1987b, 1993). Recent surveys of ichthyosaurs with soft tissue preservation are by Martin *et al.* (1986) reviewing the Barrow-upon-Soar material, Martill (1993) reviewing English and German material, and Riess and Frey (1985) incorporating a comprehensive bibliography of ichthyosaurs including exceptionally preserved specimens.

MATERIAL

The septarian concretion containing the new specimen was discovered by Mr Chris Moore of Charmouth, on the foreshore in front of the Black Ven landslip between Charmouth and Lyme Regis in Lyme Bay, Dorset (O.S. Grid Reference approximately SY 356931). The lithology and the presence of small *Asteroceras* sp. suggests that the concretion is from the *obtusum* Zone of basal Upper Sinemurian age. Detailed lithological sections for the Lias at Lyme Bay were given by Lang (1914, 1924). The specimen is now housed in the collections of the Yorkshire Museum and is registered as YORYM 1993.338.

The septarian concretion is water-worn and incomplete and composed of a hard, dark grey carbonate mudstone. It measures 340 mm by 270 mm. The plane of splitting passes through the plane of the soft tissue and skeleton of the caudal region of a small ichthyosaur. Septarian cracking is slight, with infills of brown calcite. A few small septarian cracks pass through the soft tissues. The specimen was prepared slightly to expose further soft tissue and the concretion has been partly reassembled (Pl. 1; Text-fig. 1).

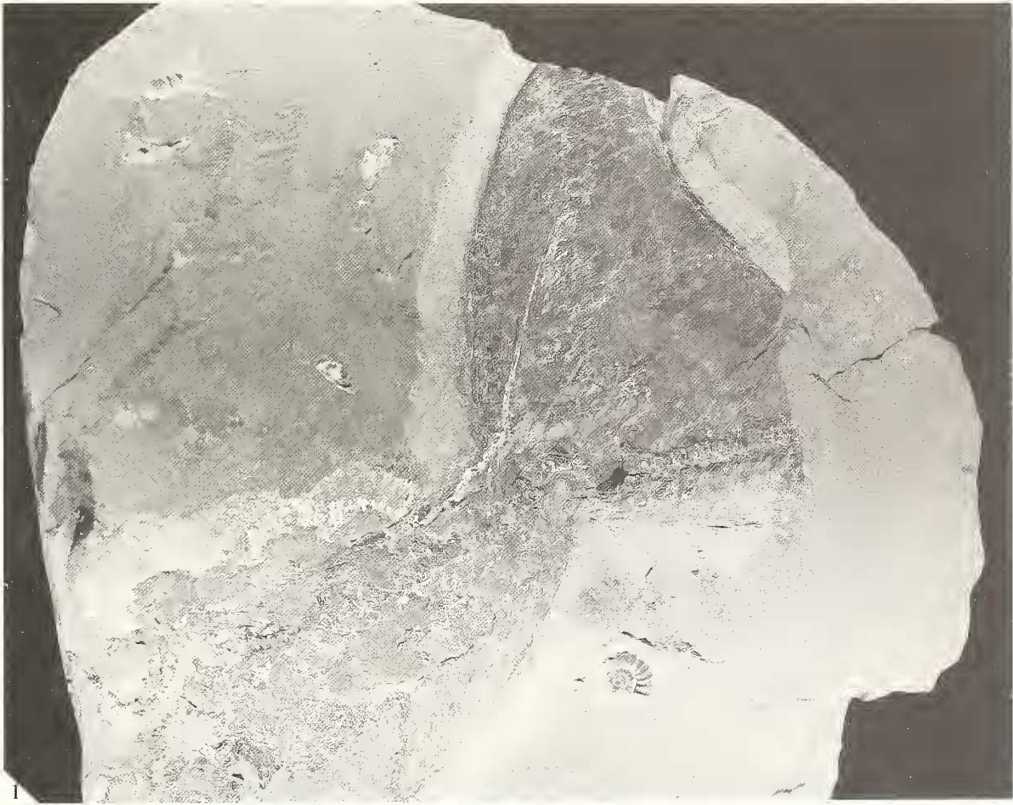
DESCRIPTION

Axial skeleton. Only the posterior portion of the axial skeleton is present. It is in articulation apart from a few slightly displaced vertebrae in the region of the tail bend. It is almost certainly part of a complete skeleton, the rest of which is presumably still in the Black Ven landslip. The vertebrae have been split and are visible in section. Ten articulated vertebrae followed by three disarticulated vertebrae are present anterior to the tail bend. Four vertebrae comprise the tail bend, followed by a series of 13 articulated vertebrae extending from the tail bend to the ventral lobe of the caudal fin. A few distal vertebrae are missing. The small size of the specimen suggests that it represents a juvenile individual.

Soft tissues. The soft tissues show the distinct outline of a lunate caudal fin and part of the posterior region of the trunk. All soft tissues are compressed and the caudal fin is twisted anti-clockwise in relation to the body as seen from the anterior. The soft tissues comprise two distinct materials: (1), a smooth, black to brown, organic material; (2), buff-coloured, slightly fibrous material, interdigitating with the black/brown material. The buff material is probably phosphatic; although no tests have been performed on it, it closely resembles

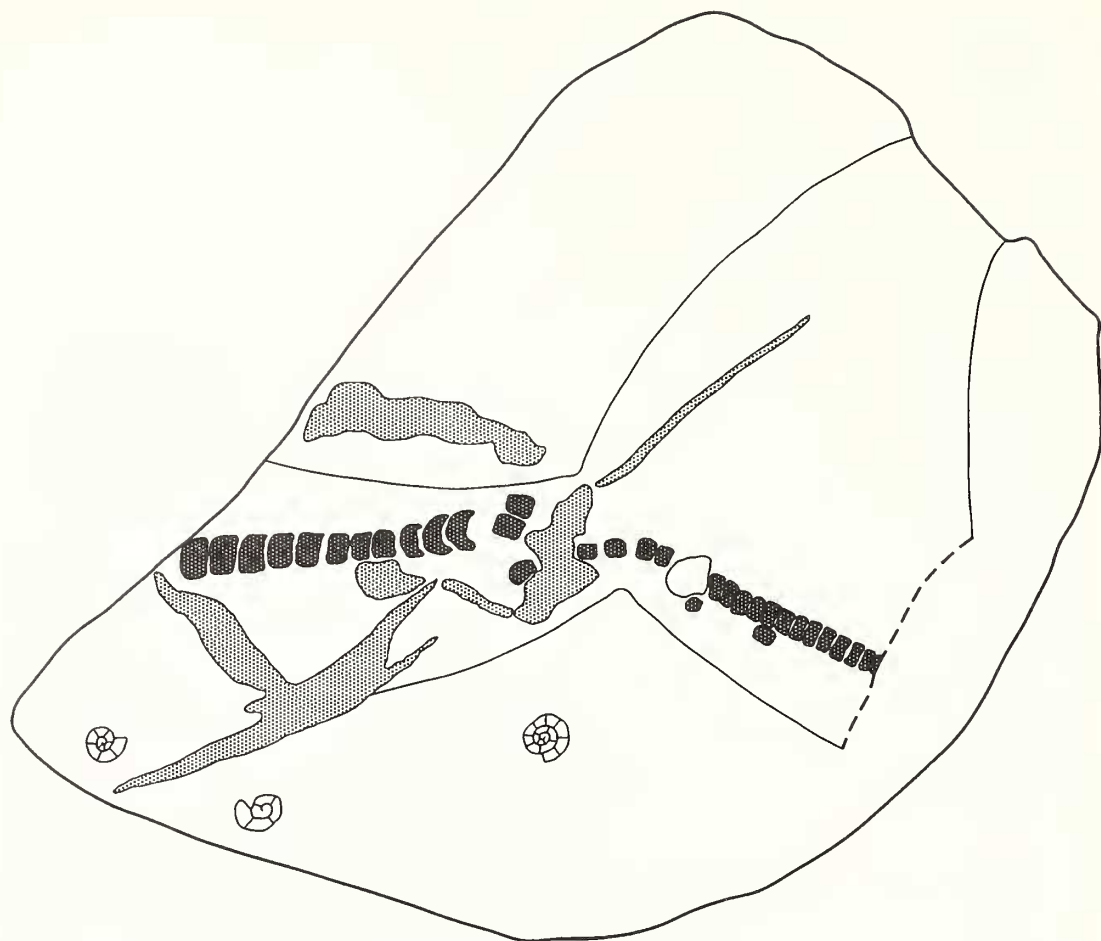
EXPLANATION OF PLATE I

The new soft tissue ichthyosaur specimen; YORYM 1993.338; Lower Lias; Black Ven, Dorset, UK.
1, *c.* $\times 0.5$. 2, high contrast photograph of caudal fin region showing areas of organic material (appearing dark) and areas of ?phosphatic material (appearing whitish); specimen photographed wet, *c.* $\times 0.75$.



2

MARTILL, ichthyosaur



TEXT-FIG. 1. The new soft tissue ichthyosaur specimen; YORYM 1993.338; Lower Lias; Black Ven, Dorset, UK. Sketch illustrating the areas of soft tissue preservation, bones (dark stipple), and late diagenetic calcite (light stipple) in septarian cracks.

phosphatic material found in Holzmaden ichthyosaurs. Both of these materials are known from the *Posidonia* Shale (Lower Jurassic, Toarcian) soft tissue ichthyosaurs (Keller 1992) and from an example of *Ophthalmosaurus* from the Oxford Clay Formation (Middle Jurassic to Upper Jurassic, Callovian–Oxfordian) of central England (Martill 1987b).

In most places the edge of the soft tissue is sharp and defines the shape of the posterior trunk and caudal fin in left lateral view. The edge of the soft tissues has been exposed by preparation, but this has not produced a spurious outline as is the case with some Holzmaden specimens (Martill 1987a, 1993). The ventral margin of the lower caudal lobe is indistinct. The tips of both dorsal and ventral lobes are missing, having extended beyond the present (eroded) boundaries of the concretion.

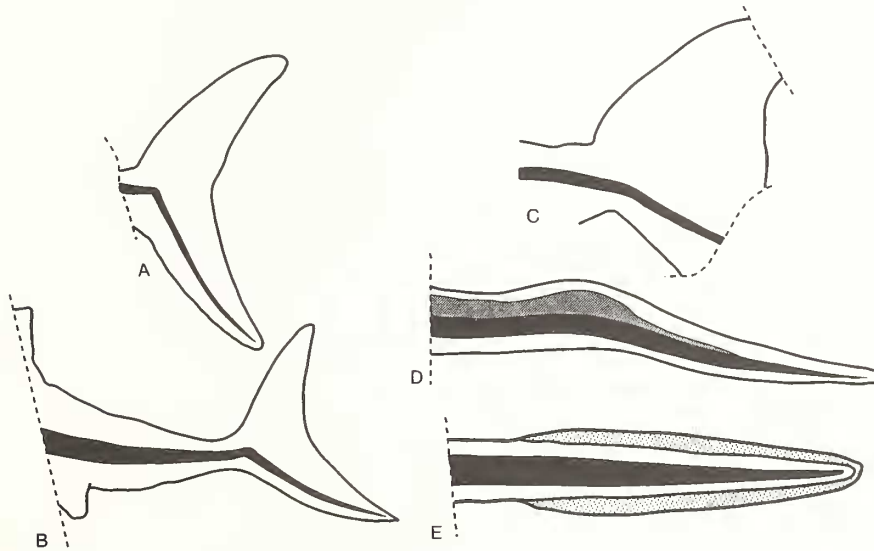
Most of the outline is defined by the distribution of the black/brown organic material. The fibrous buff material is restricted to narrow zones within the central region of each lobe. Buff material is found adjacent to the ventral and dorsal surface of the vertebral column within the lower lobe of the caudal fin. The fibrous nature, colour and aspect of its distribution suggest that this material is most likely to be the phosphatized musculature of the axial skeleton. It resembles phosphatized muscle tissue from fishes of the Cretaceous Santana Formation of north-east Brazil (Martill 1988).

DISCUSSION

Numerous authors have reported on the occurrence of ichthyosaurs with soft tissues preserved in the Jurassic of England (see above for references). Most of these remains are fragmentary, and none has soft tissues associated with the caudal skeleton.

The new specimen is the oldest known ichthyosaur caudal fin outline. It demonstrates that the complete, lunate outline of the 'typical' ichthyosaurian caudal fin had been achieved by the Sinemurian, an idea that could previously only be postulated on the basis of skeletal elements alone. In addition, the preserved musculature in the dorsal lobe of the new specimen suggests that some degree of control of the shape, rigidity and position of the upper lobe of the tail occurred during locomotion.

It remains unclear as to how the lunate caudal fin of ichthyosaurs evolved. Many Triassic ichthyosaurs, e.g. *Shonisaurus*, had straight tails (Text-fig. 2E), with no distal downturn of the



TEXT-FIG. 2. Caudal fin outlines of ichthyosaurs; vertebral column outlined in black. A, deeply forked caudal fin outline of ichthyosaur gen. et sp. indet., from the Solnhofen Limestone, Upper Jurassic of Bavaria; outline drawn from photograph in Martill (1993, fig. 13). B, caudal fin outline of *Stenopterygius quadriscissus* from the *Posidonia* Shale, Lower Jurassic of Baden-Württemberg, Germany; after illustration in Hauff Museum guide. C, YORYM 1993. 338; outline of caudal fin of the new specimen from the Sinemurian of Dorset. D, supposed caudal fin outline of the Triassic ichthyosaur *Mixosaurus* sp. from Grenzbitumenzone, Ticino, Switzerland; note that the upper lobe of the tail is supported by extended neural spines (shaded dark grey) and that the caudal vertebrae are only slightly downturned. E, supposed outline of caudal fin of the Triassic *Shonisaurus* from Nevada, USA; note that the vertebral column is straight; there is no direct evidence for the dorsal and ventral fins, but biomechanical constraints require them (Riess 1986). Figures D and E are from Riess (1986).

vertebral column (Riess 1986; McGowan 1992). These animals are assumed to have used their tails for lateral undulatory locomotion, as do modern crocodilians (McGowan 1992). The Triassic ichthyosaur *Mixosaurus* has a slightly downturned distal portion of the vertebral column, and also has neural spines of increased height over the region of the tail bend (Text-fig. 2D). This presumably supported an upper caudal lobe, but how much this may have extended beyond the skeleton is unknown as soft tissue specimens do not exist. There is no evidence for increased neural spine height in any of the Lower Jurassic ichthyosaurs, suggesting perhaps that the modified caudal fin of

Mixosaurus was not a precursor to the Jurassic ichthyosaur tail condition, as postulated by Jaekel (1904).

The downturn of the vertebral column in the new specimen is only about 25° (Text-figs 1, 2c), although it is difficult to measure accurately because of torsion of the trunk. *Stenopterygius* from the *Posidonia* Shales (Toarcian) consistently has a downturn of between 30° and 50° (Text-fig. 2b), whereas the Solnhofen (Upper Jurassic, Tithonian) ichthyosaur tail shows a downturn approaching 80° (Text-fig. 2a). It is tempting to view this as a gradual increase in the degree of downturn of the vertebral column through the Jurassic, reflecting perhaps increased swimming efficiency, and a response for catching faster-swimming soft-bodied cephalopods and perhaps fish.

A surprising aspect of all ichthyosaur soft tissue specimens is the lack of preservation of typical reptilian scales. This might be attributed to the preserved outline being: (1), a prokaryote mat replacement, resulting in loss of original structural detail; an idea suggested by Martill (1987c) but challenged by Keller (1992); (2), the *in situ* preservation of degraded organic matter preserving only the shape of the ichthyosaur, but no detail; (3), the preservation of a part of the integument below the scaly epidermis; or (4) the preservation of an integument which lacked reptilian scales. The discovery of dinosaur integument from the same formation at a nearby locality (1 km distant) in which typical reptilian scales are well-preserved (Martill 1991) suggests that ichthyosaurs probably lacked typical reptilian scales. Rather than scales, a feature present on the integument of a number of *Posidonia* Shale soft tissue specimens as well as on a Barrow-upon-Soar specimen, is small, ripple-like ridges (Martill 1993, pl. 5, figs 1–6). Although these features may represent artefacts of preservation, they could be original, perhaps having assisted in locomotion, or alternatively, in limiting the opportunities for parasite attachment. Unfortunately these features are not observed on the new specimen.

Acknowledgements. I thank Mr Paul Ensom of the Yorkshire Museum for bringing the new specimen to my attention, and the trustees of the Preservation of Industrial and Scientific Material fund (PRISM) for purchasing the specimen, and thus saving it for the scientific community at large. I would like to thank Drs Dino Frey, Jurgen Riess, Arthur Cruickshank and Mr John Martin for thought-provoking discussion. One referee was frank, but nevertheless helpful.

REFERENCES

- ANDREWS, C. W. 1924. Note on an ichthyosaurian paddle showing traces of soft tissues. *Proceedings of the Zoological Society, London*, **1924**, 533–537.
- BAUER, F. 1898. Die Ichthyosaurier des Oberen Weissen Jura. *Palaeontographica*, **44**, 283–328.
- BAUR, G. 1895. The fins of ichthyosaurs. *Journal of Geology*, **3**, 238–240.
- BÖTTCHER, R. 1889. Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stuttgarter Beiträge zur Naturkunde*, Ser. B, **155**, 1–19.
- BROILL, F. 1942. Verfestigungen im Integument der Ichthyosaurier. *Sitzungsberichten der Bayerische Academie der Wissenschafte, Mathematisch, Naturkunde, Abteilungen*, 37–52.
- BUCKLAND, W. 1836. *Geology and mineralogy (Bridgewater Treatise)*. London.
- COLES, H. 1853. On the skin of *Ichthyosaurus*. *Quarterly Journal of the Geological Society, London*, **9**, 79–81.
- DAVIES, W. 1864. The skin of reptiles in a fossil state. *Geological Magazine*, **1**, 248.
- DELAIR, J. B. 1966. Unusual preservation of fibrous elements in an ichthyosaur skull. *Nature*, **5062**, 575–576.
- FRAAS, E. 1892. Ueber einen neuen fund von *Ichthyosaurus* in Württemberg. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, **2**, 87–90.
- HAUFF, B. 1921. Untersuchun der Fossilfundstätten von Holzmaden im Posidonienschiefer des Oberen Lias, Württembergs. *Palaeontographica*, **64**, 1–42.
- HAUFF, B. and HAUFF, R. B. 1981. *Das Holzmadenbuch*. Hauff Museum, Holzmaden, 136 pp.
- JAEKEL, O. 1904. Eine neue darstellung von *Ichthyosaurus*. *Deutschland Geologische Gesellschaft*, **56**, 26–34.
- KELLER, T. 1976. Magen- und Darminhalte von Ichthyosauriern des suddeutschen Posidonienschiefers. [Stomach and intestinal contents in ichthyosaurs of the Toarcian *Posidonia* Shales]. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **5**, 266–283.

- 1992. 'Weichteil-Erhaltung' bei grossen vertebraten (Ichthyosaureirn) des Posidonienschiefers Holzmadens (Oberer Lias, Mesozoikum Süddeutschland). *Kaupia*, **1**, 23–62.
- LANG, W. D. 1914. The geology of Charmouth cliffs, beach and foreshore. *Proceedings of the Geologists' Association, London*, **25**, 293–360.
- 1924. The Blue Lias of the Devon and Dorset coasts. *Proceedings of the Geologists' Association, London*, **35**, 169–185.
- LYDEKKER, R. 1889. On an ichthyosaurian paddle showing the contour of the integument. *Geological Magazine*, **6**, 388–390.
- MANTELL, G. A. 1851. *Petrifactions and their teachings, or a handbook to the organic remains of the British Museum*. London, 496 pp.
- MARTILL, D. M. 1987a. Ichthyosaurs with soft tissues: additional comments. *Transactions of the Leicester Literary and Philosophical Society*, **81**, 35–45.
- 1987b. A taphonomic and diagenetic case study of a partially articulated ichthyosaur. *Palaeontology*, **30**, 543–555.
- 1987c. Prokaryote mats replacing soft tissues in Mesozoic marine reptiles. *Modern Geology*, **11**, 265–269.
- 1988. Preservation of fish in the Cretaceous of Brazil. *Palaeontology*, **31**, 1–18.
- 1991. Organically preserved dinosaur skin: taphonomic and biological implications. *Modern Geology*, **16**, 61–68.
- 1993. Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia*, **2**, 77–97.
- MARTIN, J., FREY, E. and RIESS, J. 1986. Soft tissue preservation in ichthyosaurs and a stratigraphic review of the Lower Hettangian of Barrow-upon-Soar, Leicestershire. *Transactions of the Leicester Literary and Philosophical Society*, **80**, 58–72.
- MCGOWAN, C. 1979. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontographica, Abteilung A*, **166**, 93–236.
- 1992. The ichthyosaurian tail: sharks do not provide an appropriate analogue. *Palaeontology*, **35**, 555–570.
- MOORE, C. 1857. On the skin and food of ichthyosauri and teleosauri. *Report of the British Association of the Advancement of Science*. (Cheltenham), 1856, **26**, 69–70.
- 1862. Notes on two ichthyosauri to be exhibited at the meeting. *Report of the British Association for the Advancement of Science*. (Manchester), 1861, **31**, 121.
- OWEN, R. 1840. A description of the soft parts and of the shape of the hind fin of the *Ichthyosaurus* as when recent. *Proceedings of the Geological Society of London*, **111**, 157–158.
- 1841. A description of some of the soft parts, with the integument, of the hind fin of the *Ichthyosaurus*, indicating the shape of the fin when recent. *Transactions of the Geological Society of London*, (2), **6**, 199–201.
- PEARCE, C. 1846. Notice of what appears to be the embryo of an ichthyosaurus in the pelvic cavity of *Ichthyosaurus (communis?)*. *Annals and Magazine of Natural History*, **17**, 44–46.
- POLLARD, J. E. 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontology*, **11**, 376–388.
- RIESS, J. 1986. Biomechanics of ichthyosaurs. 199–205. In RIESS, J. and FREY, E. (eds). *Konstruktionsprinzipien lebender und ausgestorbener reptilien*. *Sonderforschungsbereich 230*, Universities of Stuttgart and Tübingen.
- and FREY, E. 1985. Literaturbericht, Bibliographie über ichthyosaurier. *Zentralblatt für Geologie und Paläontologie*, **2**, 1/2, 7–20.
- TAYLOR, M. A. 1987. Reinterpretation of ichthyosaurs' swimming and buoyancy. *Palaeontology*, **30**, 531–535.
- WHITEAR, M. 1956. On the colour of an ichthyosaur. *Annals and Magazine of Natural History*, **9**, 742–744.

DAVID M. MARTILL

Department of Geology
University of Portsmouth
Burnaby Road
Portsmouth PO1 3QL, UK

Typescript received 14 December 1993

Revised typescript received 15 September 1994